SCIENCE

Dolphin Lung Collapse and Intramuscular Circulation During Free Diving: Evidence from Nitrogen Washout

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Dolphin Lung Collapse and Intramuscular Circulation
During Free Diving: Evidence from Nitrogen Washout

Abstract. *Intramuscular nitrogen tensions in* Tursiops truncatus *after a schedule of repetitive ocean dives suggest a lung collapse depth of about 70 meters and suggest that intramuscular circulation is maintained during unrestrained diving in the open ocean. Therefore, the bottle-nosed dolphin is not protected by lung collapse from the decompression hazards of dives to depths shallower than 70 meters.*

Ocean diving studies with a trained dolphin have shown that dolphins may be protected from decompression sickness by alveolar collapse during dives deeper than about 100 m (*1*). Recent studies have shown that dolphins dive more frequently to depths shallower than 100 m (*2*). Therefore, we decided to investigate tissue nitrogen accumulation after a long series of such shallow dives.

A Medspect MS-8 medical mass spectrometer (Searle Scientific Research Instruments Corp., Baltimore) (*3*) was used in this study to monitor intramuscular nitrogen washout after diving. This spectrometer measures the minute amounts of gases that continuously diffuse through a Teflon membrane enclosing a vacuum chamber at the end of an implantable catheter. The gases then enter the mass spectrometer in quantities proportional to their partial pressures.

Two bottle-nosed dolphins named Blue and Brown were trained to dive repetitively for about 1 hour in the open ocean to a depth of 100 m, as depicted in Fig. 1. Descent, ascent, and surface interval times were recorded for each of the 25 dives made by Blue and the 23 dives by Brown. Mean dive time was about $1^{1}/_{2}$ minutes, with about 1-minute surface intervals. During surface intervals, the ventilation rate of the dolphins was about ten breaths per minute. After completion of a dive series, the catheter from the spectrometer was inserted, trans-
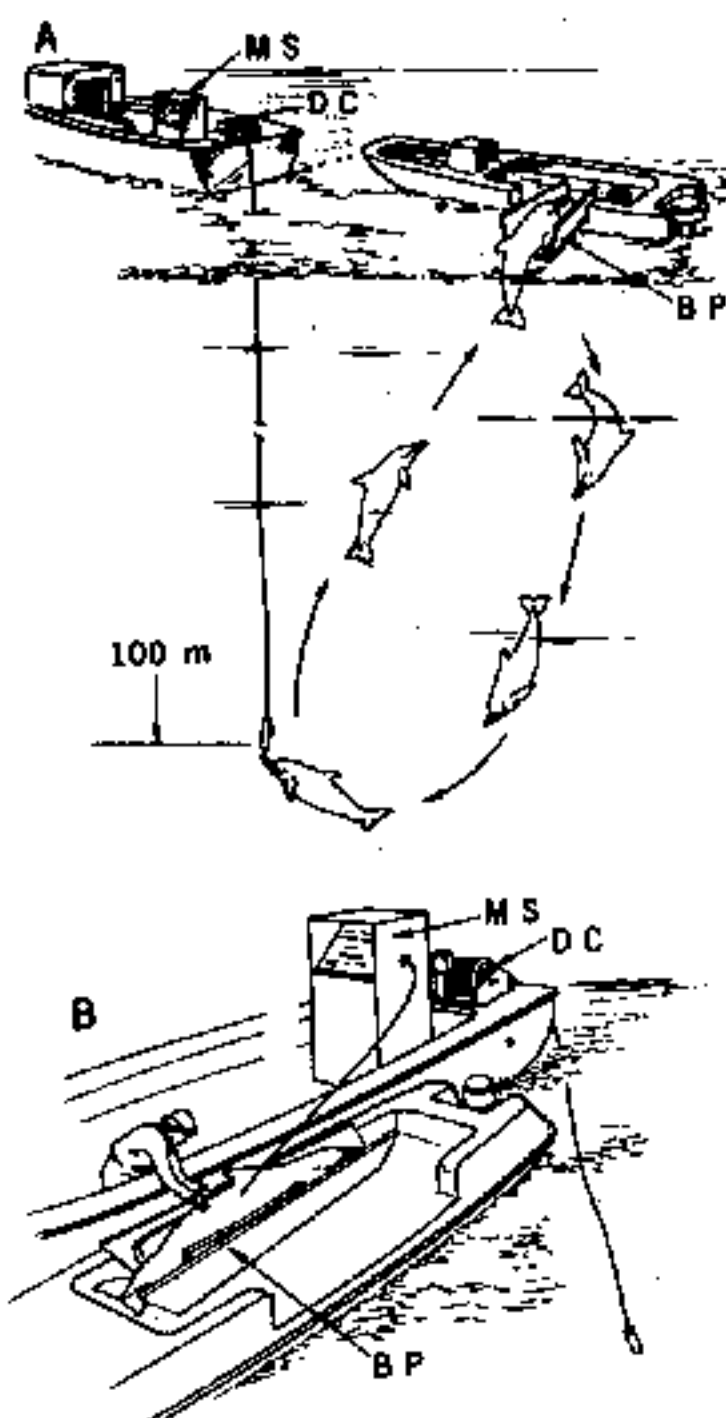

Fig. 1. (A) Each dolphin made multiple dives to a depth of 100 m to press a switch at the end of the dive cable (*DC*). After each dive it returned to the boat for a food reward during an interval of 45 seconds, after which it was commanded to dive again. After completion of the last dive, the dolphin jumped onto the beaching pad (*BP*). (B) The small boat containing the dolphin on the beaching pad was brought alongside the larger craft and the mass spectrometer (*MS*) probe was inserted. The animals remained in this position while the N_2 washout was measured.

cutaneously, directly into dorsal epaxial muscle tissue. Stable readings were obtained within about 8 minutes after the dolphin's final surfacing, and gas tensions were recorded at 30-second intervals thereafter.

Results are shown in Fig. 2. Linearly extrapolating the washout data backward to the time at which the dolphins last surfaced from the dive series, we estimate that after the hour of repetitive dives to 100 m, the intramuscular N_2 tension in Blue had increased to about 1600 τ (τ = mm-Hg), and in Brown to 1300 τ. If the absorption of nitrogen is considered to be time-symmetric with its elimination—that is, the half-times observed during washout are equal to those that would be observed during washin—then, using a procedure described by Workman (4), we can predict what the nitrogen tension in the muscle should be after a known repetitive dive schedule. Assuming the ascent rate to be constant and equal to the descent rate during any one dive, we used the equation

$$P_{N_2} = H_0 + R \times \left(t - \frac{h}{\ln 2}\right) +$$
$$\left(P_0 - H_0 + \frac{R \times h}{\ln 2}\right) \times 2^{-t/h}$$

where $H_0 = 0.78 \times$ (initial hydrostatic pressure $-$ 46 τ), $R = 0.78 \times$ descent rate (negative for ascent), h is the half-time, t is time, P_0 is the initial tissue N_2 tension, and P_{N_2} is the final tissue N_2 tension.

For the dive schedules observed, the absorption in a tissue with a 5.2-minute half-time and an initial tension of 580 τ should have resulted in a N_2 tension of about 2400 τ in Blue, and the 6.6-minute half-time should have resulted in an even higher P_{N_2} of about 2900 τ in Brown. We next recalculated the absorption that would have occurred during the dive schedules with a constraint that N_2 transport was stopped below various depths. To achieve the final tensions that were extrapolated to in Fig. 2, N_2 transport to the muscle was interrupted at about 70 m in Blue and about 65 m in Brown. A physiological interpretation of this calculation is that blood previously equilibrated with alveolar gas is not aerated at all below this depth. This first approximation of pulmonary collapse may underestimate the depth of complete atelectasis, since the isolation of pulmonary air from circulation may be gradual. A gradual decrease in N_2 transport, however, could be incorporated within this calculation.
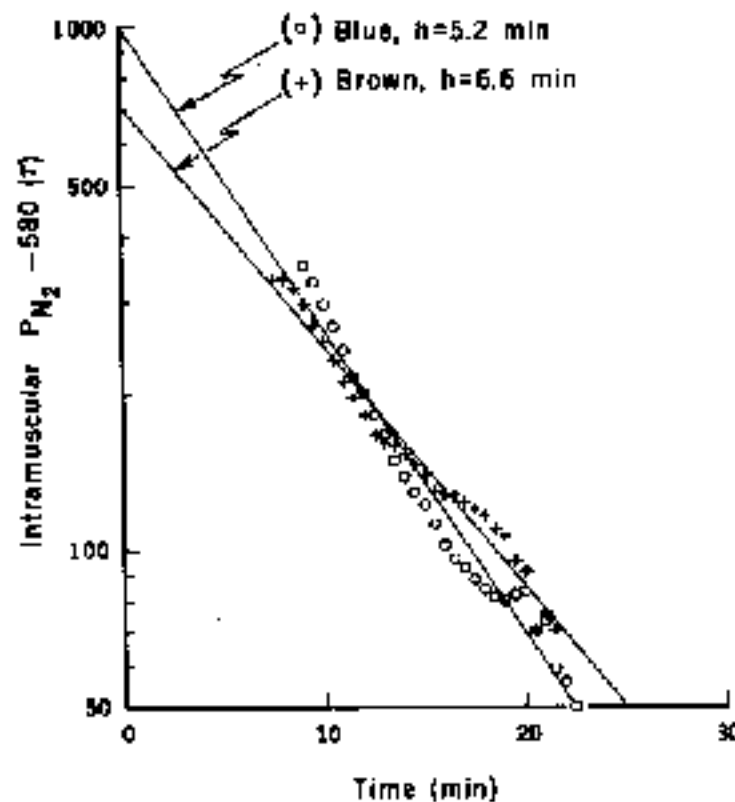
The assumption of symmetric absorp-

Fig. 2. Nitrogen washout from muscle tissue plotted semilogarithmically as the tension differential above 580 τ, which was independently determined to be the normal partial pressure of N_2 in unloaded tissue. The half-time, h, of a tissue is the time it takes for the tissue to absorb or eliminate gas to half the tissue's saturated tension after a step change in diving pressure; $h = -\log 2/\text{slope}$. Intercepts and half-times were determined by linear regression.

tion and elimination within tissue is supported by other animal experiments (5), although gas uptake in diving dolphins may be slowed by diminished perfusion as well as progressive pulmonary collapse. Tissue washouts over periods longer than 30 minutes may need to be described multiexponentially, indicating that intratissue diffusion may become a significant factor in N_2 transport.

Measurement of blubber nitrogen tensions lower than those for muscle resulted in significantly shallower lung collapse depths when calculated with the Workman formula. We interpret this as an indication that perfusion of the blubber is not maintained as effectively as that of the muscle during diving. We have evidence that gas depletion affects our measurement within blubber, and although the probe must necessarily sample damaged tissue, we believe our measurements of intramuscular tensions are representative values since stable surface values averaging about 580 τ have been recorded for hours.

Preferential shunting of blood from the extremities to the great vessels during diving permits the oxygen stores in the blood to be used almost exclusively to perfuse the heart and brain and thereby provides for long dive durations. The concept of an almost reflex-like circulatory redistribution for selective oxygenation of sensitive tissues at the expense of those having greater anaerobic capability has received considerable atten-

tion. It is well established that there is no effective muscle circulation in the restrained seal on immersion (6), although the bottle-nosed dolphin has not displayed so marked a circulatory adjustment for diving (7). We suggest that even though marine mammals have the capability for such peripheral vasoconstriction, they maintain an effective intramuscular circulation when diving free in an open ocean environment.

Two physiological adaptations to diving commonly ascribed to dolphins are (i) alveolar collapse at a relatively shallow depth (1) and (ii) profound peripheral vasoconstriction during diving (6, 7). Our measurement of nitrogen tensions in the bottle-nosed dolphin *Tursiops truncatus* after a known schedule of repetitive free dives provides evidence of this first adaptation; it does not support the latter phenomenon of circulatory shutdown in muscle at the onset of diving, since obtaining the observed N_2 tensions (two to three times the normal, surface levels) required effective intramuscular circulation during diving and pulmonary collapse at a depth greater than 70 m. Therefore, bottle-nosed dolphins are not protected by lung collapse from the decompression hazards of dives to depths shallower than 70 m, and the mechanism by which dolphins avoid decompression sickness on dive schedules known to produce the syndrome in man (8) is not yet completely understood.

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References and Notes

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